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On the anomalous splitting of the rhizome and root of Delphinium scaposum

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(WITH PLATES 13 and 14)

Delphinium scaposum, first named by Greene,* is one of the xerophytic forms of the Ranunculaceae. The material used in this investigation was collected at the Desert Laboratory at Tucson, Arizona, under the kind direction of Dr. D. T. MacDougal of the Carnegie Institution. It was carefully killed at that time, and proved most satisfactory for anatomical study.

As to its distribution, Huth,† who names it *Delphinium decorum β scaposum* (Greene) Huth, reports that it was mentioned by Parry, 1874, as found in southern Utah, and by Pringle, 1883, in the Arizona hills near Tucson, the same territory from which this material was sent. Greene records its presence in the hill country between the Gila and San Francisco rivers, May 25, 1880, and says that Dr. Asa Gray informed him that Professor Newberry obtained what appeared to be the same, south of the Diamond River in Arizona.* In this same account, Greene gives the only adequate description of the plant, which I quote in part, as I have no acquaintance with the living form. "Leaves all radical, rather fleshy, pubescent, 3-parted, the divisions broadly cuneate, 3–5-cleft or toothed, the teeth ending in a callous point, racemose at summit, pedicels as long as the deep azure flowers; spur incurved, root a

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*E. L. Greene. New Species of Plants from New Mexico. Bot. Gaz. **6**: 156–158. 1881.

†Ernst Huth. Die Delphinium-Arten der Vereinigten Staaten von Nord-Amerika. Abhand. und Vorträge Gesammtgeb. Naturw. **4**^{3}: 9. 1892.

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cluster of thickened fleshy fibres. . . . An interesting species as combining the leafless stem of the scarlet flowered Californian *D. rudicaula* with the deep blue flowers of *D. azureum.*"

The aerial part consists of leaves whose long petioles arise spirally from a restricted underground shoot, and blossoms borne on long stalks. These flourish in the brief rainy season and then die back, and the next year's leaves and flowers originate from a terminal bud, or from buds found one in the axil of each foliage leaf. The perennial part of the plant is subterranean, and is of the nature of a rhizome with roots attached. This is the part that was particularly studied here.

On examination of this portion of the plant body, of several different specimens, the most apparent characteristic common to all is the splitting up into separate members of the rhizome and root (FIG. 1). There is no regularity about the number or arrangement of the resulting columns, nor is their origin as separate individuals at an equal distance from the base of the annual shoot. In one case a specimen will appear like a miniature tree trunk covered with a dark brown barklike formation which easily crumbles off. This trunk continues down as one united column for an inch, and then abruptly divides into two unequal parts. If a cross section of the main trunk were examined immediately before this separation (FIG. 2) it would show a peripheral circle made up of single columns (in cross section), the central space and divisions between which are filled with this same loose brown necrotic tissue that surrounds the outside. Shallow grooves can be distinguished running longitudinally along the trunk, and continuing more deeply cleft in each of the two divisions, so that the first consists apparently of four, the second of seven united columns.

Following these two divisions down a short distance, we find them resolving themselves into their component members, or groups of two or three, and separating from each other. Each of these ultimate branches may continue as it is, or may later divide after it has attained a certain secondary growth in thickness. Occasionally a splitting apart occurs for a short distance and is followed by a complete union of these same members into one strand, which leads to the just conclusion that the phenomenon is one of splitting of mature organs rather than a peculiarity in

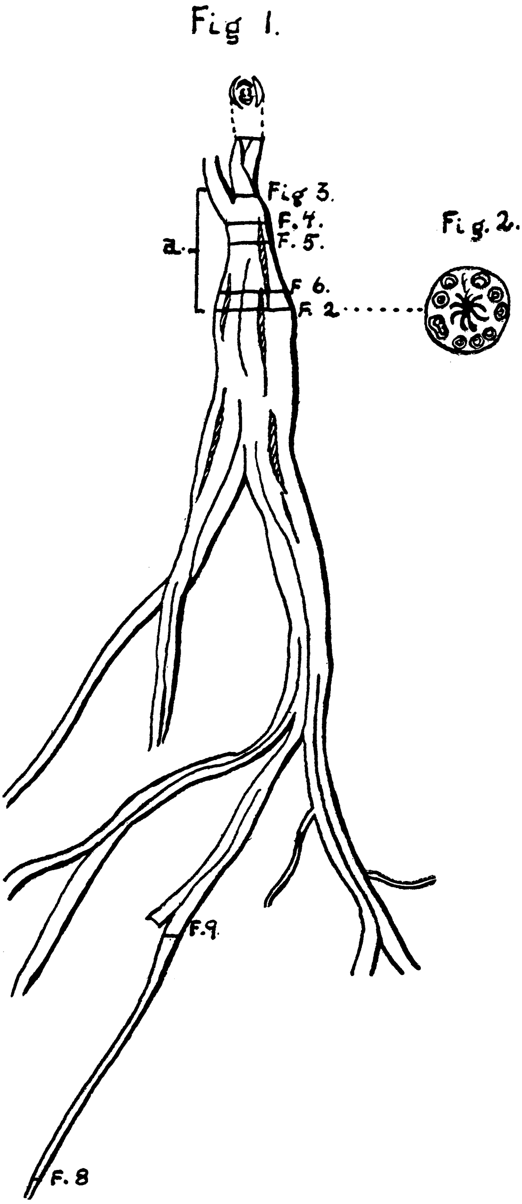

FIG. 1. Rhizome and root (natural size), showing where successive cross sections are taken.

FIG. 2. Cross section as indicated on FIG. 1, showing origin of separate columns. Necrotic central region.

regular growth development. Consequently, the whole appearance of the underground part of *Delphinium scaposum* is that of a highly complicated "cluster of fleshy roots" in part of their extent bound together like a cable, in part ramifying about irregularly through the soil and thus obtaining a wide spread. In another specimen, splittings occur almost immediately below the annual shoot. These split-off pillars need not necessarily be circular in cross section, for as often columns are found sickleform in cross section. (Later examination reveals the fact that whereas the circular sections contain but a single vascular bundle and its secondary thickenings, the sickleform ones invariably have two or more distinct primary bundles with the rays between.) These practically always divide ultimately into members assuming this same circular appearance.

Since there is no set order followed that can be discovered from external characteristics, the phenomenon of this splitting must be investigated internally. The only available matter published on this subject is a series of articles by Jost appearing in the Botanische Zeitung, 1890, and all references to the various forms he investigated will be referred to by page without repeating the entire reference each time after the first. My most satisfactory work was done with free-hand sections, treated with KOH and mounted in glycerine. Though some successful imbedding in paraffin was accomplished through the carbon disulphid process, the stained slides were more difficult to elucidate than the others, and proved of less value for actual study.

If we take a specimen like FIG. 1*a*, which shows, natural size, a piece of the rhizome and the leaf bases of the aerial shoot, and examine successive cross sections, we shall be able to trace this separation from the individual main stem of the aerial shoot down to the complete circle of separate columns, as shown in FIG. 2. The places where all successive sections described in this series are cut, are indicated on FIG. 1. The first section (PLATE 13, FIG. 3) shows a regular primary stem structure. The hollow center is surrounded by four rows of parenchyma cells, outside of which is a circle of separate open collateral bundles. These primary bundles consist of xylem, cambium, phloem, with a heavy stereome cap, outside of which are five rows of cortical parenchyma cells, surrounded by a single-layered epidermis. Jost mentions the fact that "the aerial stems of so many Ranunculaceae show only a slight growth in thickness and develop no interfascicular cambium."* Farther down we find a complete cambium ring, through the activity of which the radial length of the primary bundles has been increased, not so much in xylem and phloem elements as in parenchyma, 4–7 rows of which are found on each side of the cambium. This has pushed the stereome cap farther out in the cortex, and we also find a periderm beginning to form to replace the epidermis. The secondary thickening in this and later sections is formed by a cambium that produces one ring of elements annually. This is anomalous to some extent, since it forms much more parenchyma than sieve or xylem ducts. The reason for this fact cannot be absolutely proved, but there may be a water storage function for all these thin-walled cells, which a xerophyte might very readily utilize. The cambium (FIG. 4) next produces weak secondary xylem elements outside of the primary xylem (which is flanked on both sides by stereome), followed by about five rows of equilateral parenchyma cells and five rows of brickshaped cells. The general change in shape suggests the spring and fall cells in wood, and probably owes its existence to the same slowing down in growth at the end of the growing season.

Outside of the cambium much parenchyma and a few sieve cells have been produced. In the outer cells of this closely packed cortex, separating it from the loose, irregular peripheral cells, appears a single row of cells with slightly thickened lateral walls, which makes a complete circle of the stem and forms an endodermis. Some of the primary cortex with its masses of stereome has become broken up, probably due in part to growth pressure from within. There is a darkening of the pith around the hollow center, which indicates necrosis of the tissues. In the next lower section (FIG. 5), which shows three years growth in thickness, we find the parenchyma which surrounds the first year xylem assuming the irregular appearance of the cortical parenchyma. A circle of cells exactly similar to the endodermis has formed inside, cutting off from the rest of the wood the xylem of the original bundles, enclosing the

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*Jost. Die Zerklüftungen einiger Rhizome und Wurzeln. Bot. Zeit. **48**: 484. Jl 1890. (On *Aconitum Lycoctonum.*)

necrotic pith. Undulations appear in the outer endodermis, one of which develops into a deep cleftlike projection through the rays between the bundles and toward the center of the stem, from which the inner endodermis extends out to meet it. By the union of these the stem is divided on one side. This phemomenon may occur simultaneously in more than one radius, thus dividing the section into several parts. But in each case this method holds good, and in each case either one radial bundle mass is separated off into a circular column, or more are cut off into a sickleform group.

In his discussion of splitting in *Gentiana cruciata*,* Jost describes the division as being due to the separation of parts, by a row of newly originating cork-covered parenchyma cells, which he calls "periderm." This he considers to be a single layer of cells that have been separated off and become corky, not in any way to be considered phellogenetic in origin. The pith also is cut off by an inner periderm originating from a cork cambium, which pushes out into the wood parenchyma between the fusion bundles in order to meet this "cortical periderm." This "periderm" as described, exactly agrees with the "endodermis" found in *D. scaposum*.

Following the invasion of the central necrotic region by the endodermis, the parenchyma isolated between the two sides of the cleft dies and forms a continuous link between the necrotic areas from center to periphery. In response to the death of the tissue there is the formation of a cork layer similar to wound periderm, which protects the living tissues inside from the decaying surrounding tissues. Jost also corroborates this interpretation when he says, in speaking of *Gentiana cruciata* and *Corydalis nobilis*,† that the periderm is the consequence of necrosis of tissues, and the necrosis of tissues in both cases must have an inner cause. We find cork formation taking place on all sides of the split-off columns.

This cast-off periderm on the outside easily disappears in the earth. But in cases where we find a complete circle of columns still seemingly bound in one trunk (FIG. 2), the rotting central "bark" cannot be cast off and necessarily accumulates. This large mass of dead material can hardly be all attributed to cork formation, from the excessive amount and comparative protection of the parts thus clothed. Part of its bulk must of necessity arise from the necrotic parenchymatous pith and primary bundles cut off in the center. And careful examination of the dead elements found here, shows ducts, spiral and reticulate, as well as many fibrous pieces made up of stereome strands.

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* Jost. Loc. cit. p. 43.

† Jost. Loc. cit. p. 476.

Jost believes that each old year's wood, as it becomes useless for water conduction or ceases to be in direct connection with the present year's annual growth, is cut off from the living functioning parts by this circular periderm formation, and dies, thus adding to the bulk of necrotic tissue and lessening the area of activity. Jost describes minutely this phenomenon in several cases. In *Gentiana cruciata*,* as secondary growth continues, forming new wood and cortex, old tissues are constantly cut off by an ever originating parenchymatous periderm and the significance of this periderm is to separate the functionless wood and bast in the rhizome and root from the living. In *Corydalis Ochroleuca*,† only those bundles are kept that are in direct union with leaf parts. The rest die off, and jagged parenchyma strands in the wood, by turning brown and dying, form the splits. In *Aconitum Lycoctonum*‡ (as in *Gentiana*) under symmetrical cork formation about the living tissues, and with parenchyma cells cut off that become corky about dying tissues, never more than two years' growth is left active. Periderms formed later are either concentric with the first or contribute to further splitting as already described. In *Sedum*,§ old years are all cut off by the periderm, and only the one youngest ring remains active. In *Delphinium*, such wholesale destruction apparently does not exist. No necrosis, cutting off bundle elements, can be found before the second year, and in no older form is less than two years' growth active.

In a rhizome showing four years of xylem (FIG. 6) the primary xylem is disintegrated, in the center directly outside of the necrotic pith region, and is cut off from all the rest of the wood by heavy cork zones that have particularly strong inner rims, and surround each a different one of the five columns of the split rhizome. Each one of these columns (PLATE 14) directly inside of the cork layer, has a circular region of irregular, loose parenchyma (not disintegrated to the extent of becoming brown, however). In this loose tissue the secondary xylem elements can be seen separated out from the third and fourth year elements, all three of which are surrounded by a complete ring of endodermis. This endodermis marks the outer limit of the regular close cortex, and may become, as secondary wood and parenchyma are produced inside, so stretched out and pushed into outer cortex, that it becomes the seat of activity for the production of a new cork region as the disintegrating cortical cells invade this central portion farther.

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*Jost. Loc. cit. pp. 444, 461.

†Jost. Loc. cit. p. 477.

‡Jost. Loc. cit. p. 490.

§Jost. Loc. cit. p. 504.

This column (as shown in PLATE 14) is not perfectly rounded. But the presence of a very active meristematic zone inside of the former inner endodermis cutting off cells on the inner side, seems to account for the final rounding off of these separate members.

Owing to the necrosis of tissues in the center of older parts, it is impossible to determine with any degree of accuracy where rhizome ends and root begins. To follow out the root changes we must begin, as in the case of the stem, with the youngest parts. The lower end of one of the final divisions, in cross section, shows a diarch root arrangement (FIG. 8), with the axial strand small but developed apparently in centripetal order, since the larger ducts are in the center, the smaller toward the outside; also since longitudinal sections show the same order of duct formation—spiral toward the outside, pitted toward the center.

Secondary thickening follows by the activity of a complete cambial ring, which cuts off collateral xylem elements and phloem opposite the primary bundle strands, and radial rows of parenchyma cells in all the remaining space. In the third layer from the outside of the regular parenchyma cells, appears the single endodermal row of cells, as in the shoot, cutting off the spongy parenchyma from the inner regions. When three years' xylem shows in a section cut farther back (FIG. 9), the central strand is surrounded by an endodermis and parenchymalike active cells. The loose cortical parenchyma invades the center through the groove made by the entering of the outer endodermis, and the root is divided. The periderm surrounds the root, and in turn each division is completely protected by an active cork layer.

There is, then, complete correspondence in the method of splitting in rhizome and root.

In general it can be said that originally in the young seedling, rhizome and root must have been continuous and undivided. As secondary thickening, accompanied by abnormal changes in central and peripheral tissues, took place, necrosis occurred in the center and to a slight extent on the outside. Longitudinal sections show that the central disintegration is very irregular, being a wide region narrowing down at each end to a small neck which opens into another larger cavity, etc. Jost claims that there is a correspondence between the leaf position and the bundle courses, and between the bundle courses and the splitting. So far as this material can be examined, there seem to be no remaining leaf traces to affect the bundle course, which is apparently straight down through the rhizome and continued in the root. But as has been mentioned before, the columns always contain finally a single bundle strand. This column must necessarily continue its own existence independently, and it is apparently quite capable of doing so, having, as it does, an active outer cambium zone, which in successive years may circle farther and farther around inside of the limiting endodermal layer, perhaps finally forming, with the meristematic parenchyma on the inside, a complete ring around the column. No material of the age I have, shows such a complete ring, but in the four year old stage we have a very close approach to this state.

To summarize briefly the order of splitting for the rhizome, which is followed exactly in the root, we can say:

1. There is regular primary shoot structure.

2. The cambium ring produces annually some xylem and phloem tissue, but much parenchyma in the normal place of these elements. An endodermis ring appears between the outermost spongy cortex and the regularly formed outer parenchyma. Periderm surrounds the whole.

3. In the third year, an inner endodermislike ring cuts off the primary xylem and parenchyma enclosing a necrotic pith, from the rest of the tissues.

4. The outer endodermis pushes down between the xylem masses, joins the inner ring of like structure, making one con-

tinuous ring about each of the segments into which the rhizome is thus divided. The tissues cut off in this way become necrotic. Columns formed are each surrounded by an active cork-forming periderm, they continue an independent existence and never exceed the number of the original bundles.

This anatomical study of the rhizome and root of *Delphinium scaposum* was carried on in the Botanical laboratories of Barnard College, Columbia University, under the direction of Dr. Herbert M. Richards, to whose inspiration and helpful suggestions the success of this investigation is mostly due. The writer wishes also to express her thanks to Dr. D. T. MacDougal for furnishing the material, and to Dr. Tracy E. Hazen and Dr. P. A. Rydberg for their assistance in determining the identity of the plant studied.

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COLUMBIA UNIVERSITY.

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Explanation of plates 13 and 14

FIG. 3. Cross section of primary aerial stem, showing regular primary structure, bundle ring, hollow center, stereome.

FIG. 4. Cross section of rhizome in second year, showing irregular outer parenchyma with groups of stereome, outer endodermal ring separating regular and irregular cortex, cambium ring between 2nd xylem and phloem, slight necrosis around hollow center. Space outside 1st xylem shows ring of "fall" parenchyma cells. Periderm formed.

FIG. 5. Cross section of rhizome in third year, showing inner endodermis cutting off xylem of first year with enclosed irregular parenchyma and necrotic pith. Outer endodermis projected between xylem strands meets inner endodermis, dividing the rhizome into two parts. Other grooves appear in outer endodermis, indicating subsequent divisions.

Fig. 10.

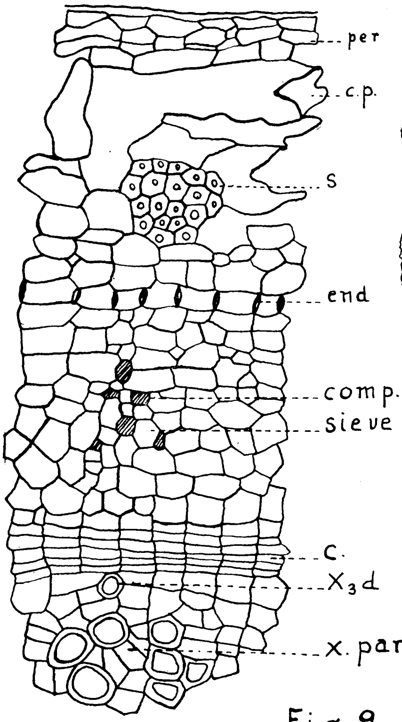


Fig. 6.

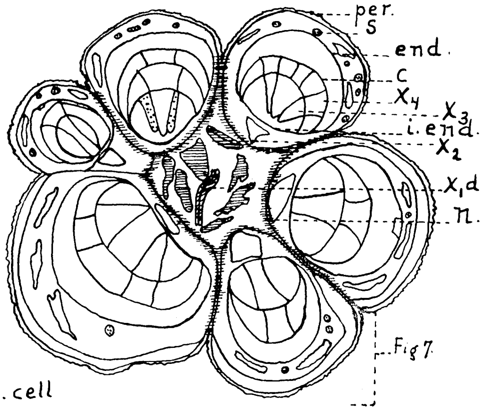


Fig. 5.

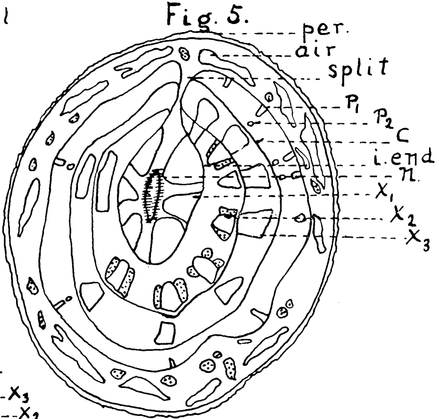


Fig. 9.

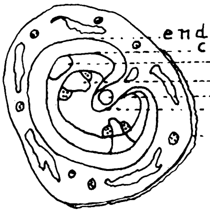


Fig. 8

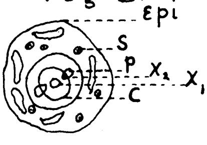


Fig. 4.

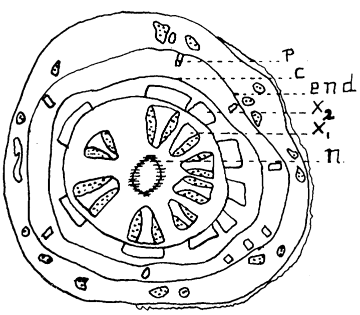
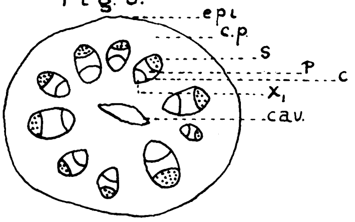


Fig. 3.



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KINGSLEY, RHIZOME AND ROOT OF DELPHINIUM SCAPOSUM

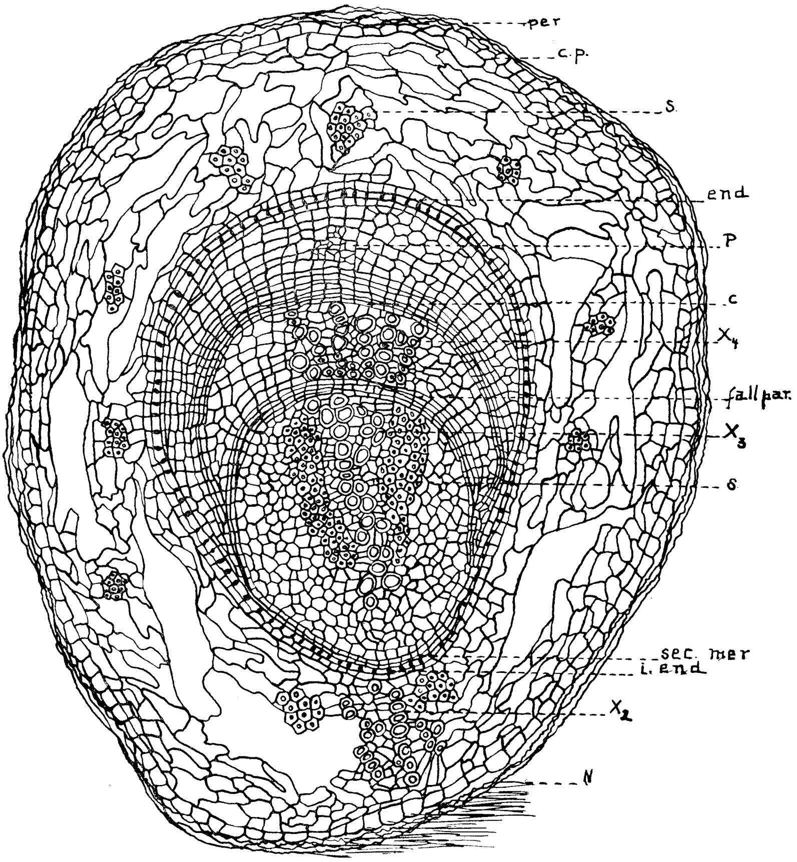

Fig. 7.

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KINGSLEY, RHIZOME OF DELPHINIUM SCAPOSUM

FIG. 6. Cross section of rhizome in fourth year, showing separate columns cut off each with separate periderm, endodermis, cambium, etc. Center of section shows necrotic parenchyma tissue and disintegrating xylem ducts of first year. Second year xylem enclosed in irregular parenchyma that eventually disintegrates. Large air cavities in among broken cells of cortex.

FIG. 7. Detail of column as indicated in FIG. 6, showing irregular parenchyma and second year xylem, endodermis and parenchyma cells of inner endodermis, and brickshaped cells of third year xylem.

FIG. 8. Cross section of ultimate division (root). Diarch order with second year collateral bundles produced, connected by cambium ring. Axial strand in center. Root endodermis like shoot.

FIG. 9. Cross section of third year root. Xylem of first year cut out by inner and outer endodermis, becomes necrotic. Groove marks first break in root. Periderm formed as in shoot.

FIG. 10. Detail of endodermis of third year rhizome.

FIG. 3–10 inclusive (except 7) magnified about 8 diameters. FIG. 7 magnified 38 diameters.

All plan drawings made with Edinger apparatus, Leitz oc. I, obj. 1a; FIG. 7, oc. I, obj. 2.

KEY

air	air cavities	*P*	phloem
c	cambium	*par*	parenchyma
c.p.	cortical parenchyma	*per*	periderm
end	endodermis	*s*	stereome
epi	epidermis	*x*	xylem; x_1—xylem of first year, etc.
i. end	inner endodermis	*x.d.*	xylem duct
n	necrotic tissue		